Nitrate uptake by size-fractionated phytoplankton on the Scotian Shelf (Northwest Atlantic): spatial and temporal variability

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Abstract. New (nitrate) phytoplankton production was estimated monthly during 1 year (March 1991– March 1992) at three stations on the Scotian Shelf, Northwest Atlantic. Samples were size fractionated to assess the uptake of nitrate by small (<5 μm) and large (>5 μm) phytoplankton. The biomass of small phytoplankton remained relatively constant over the year, whereas that of the large size fraction was high in early spring and low during the remainder of the year. Monthly variations in nitrate uptake were similar for the two size fractions, suggesting that both small and large phytoplankton used nitrate when available. It follows that, outside the spring bloom, new production was largely due to the small fraction. Our results do not support the notion that new production is associated with large phytoplankton and regenerated production with small phytoplankton.

Introduction

Biological oceanographers usually consider that primary production, at least in oceanic waters, is controlled by the availability of dissolved nitrogen in the euphotic zone (e.g. Howarth, 1988; Codispoti, 1989). Dugdale and Goering (1967) classified dissolved nitrogenous nutrients as new nitrogen (oxidized forms: nitrate, nitrite) and regenerated nitrogen (reduced forms: ammonium, urea). It is generally accepted that new nitrogen mainly comes from the deep ocean, as a result of vertical mixing, whereas regenerated nitrogen is produced by biological processes within the euphotic zone. This dichotomy concerning the sources of nitrogenous nutrients may be an oversimplification, given that it does not take into account nitrogen fixation and atmospheric transport of nitrate and ammonium (e.g. Eppley and Peterson, 1979; Legendre and Gosselin, 1989).

In theory, the amount of organic matter exported out of the euphotic zone should be in mass balance, at appropriate time and space scales, with the amount of production fuelled by new nitrogen (e.g. Dugdale and Goering, 1967; Eppley and Peterson, 1979). It has also been suggested that large and small phytoplankton do not have the same potential for export out of the euphotic zone (e.g. Cushing, 1989; Legendre and Le Fèvre, 1989). According to Legendre and Le Fèvre (1989), the type of phytoplankton production (large or small cells) and its fate (export or recycling) are controlled by hydrodynamic processes.

When nitrate concentrations are high (upwelling areas or early spring in coastal areas and on continental shelves), primary production is dominated by large phytoplankton. On the contrary, in oligotrophic areas or periods of the year, nitrogen is mainly found in reduced form and primary production is driven by small phytoplankton (Eppley and Peterson, 1979; Malone 1980). Moreover, maximum abundances of large and small cells generally occur at different times of the year (e.g. Cushing, 1989) or depths (Goldman, 1988). Harrison (1990) reported the

presence of a productivity maximum shallower than the chlorophyll maximum as a general feature in coastal and oceanic waters. He suggested that the first maximum is fuelled by regenerated nitrogen, whereas the second reflects the upward diffusion of NO_3 into the surface mixed layer. According to these observations, large phytoplankton have been associated with new nitrogen and small phytoplankton with regenerated nitrogen. This idea tends to be corroborated by the concept of preference. Even if, in general, phytoplankton seem to prefer reduced forms of nitrogen (e.g. McCarthy *et al.*, 1977), cells with different sizes may exhibit different preferences for a nitrogen form, i.e. small and large cells tend to prefer reduced and oxidized forms of nitrogen, respectively (e.g. Probyn and Painting, 1985; Harrison and Wood, 1988; Probyn *et al.*, 1990). However, Chisholm (1992) rejected the concept of preference and put forward the idea that 'the dominance of larger cells in areas enriched with NO_3 does not appear to be a result of a causal link between cell size and preference for either nitrate or ammonium'. It follows that the relationship between nitrogen form and cell size is probably less clear cut than previously thought, and probably results from the interaction between several factors, such as the size of cells, time of the year, depth and stratification.

The present study focused on the links between phytoplankton size and new production. We estimated the uptake of new nitrogen (nitrate) by two size fractions of phytoplankton (<5 and >5 μm) during an annual cycle. The hypotheses tested were that large and small phytoplankton are segregated in time and space, and that large phytoplankton are responsible for the bulk of new production.

Method

Sampling and laboratory analyses

Sampling was conducted monthly at three stations on the Scotian Shelf, Northwest Atlantic (Figure 1), from March 1991 through March 1992. The stations were chosen to be representative of different hydrodynamic and biological conditions. Station A was located at the shelf break, where it was assumed that waters were generally upwelled; station B was located on the northeastern part of the shelf and was assumed to be representative of average conditions on the shelf. The position of station C was moved from month to month in order to track conditions existing in the centre of an anticyclonic circulation, on Sable Island bank.

At each station, samples were collected at 10 optical depths over the euphotic zone, at noontime ± 2 h, using 8 l Niskin bottles. The optical depths ranged from 100 to 1% of surface irradiance, corresponding to 10 irradiance levels in incubators on board the ship. The light source for incubation was a 400 W super metal halide Optimarc lamp (Tungten Products Corp.; spectrum close to that of white light; Mouget *et al.*, 1992) in front of which blue plexiglass was placed to simulate the underwater light. The incubators were cooled by surface water circulation. Samples were pre-screened on 333 μm mesh and kept in dark thermos containers (Coleman) until the beginning of measurements (within 1 h of sampling). For each depth, two 1 l flasks containing 900 ml of sample were inoculated with ^{15}N-labelled NO_3. Nutrient concentrations were not analysed on board. Water samples were filtered on Whatman GF/F and frozen until analysis with an autoanalyser
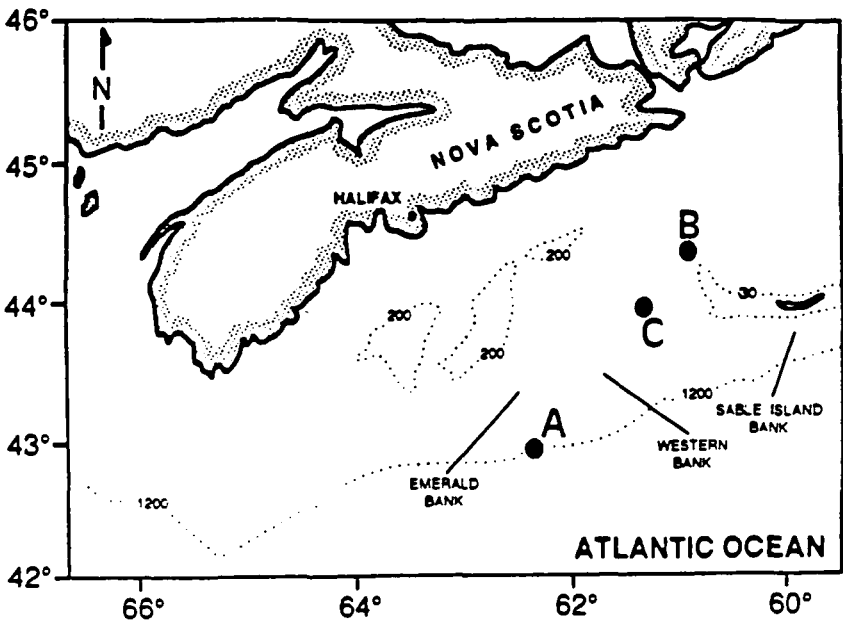
Fig. 1. Map of the Scotian Shelf showing the location of the sampling stations. The position of station C was moved each month, but it was always located in the same general area and is thus represented as a fixed station.

(Alpkem) following Parsons *et al.* (1984). Because nutrients were not analysed on board, between 0.1 and 1 μmol K^{15}NO$_3$ was added to each incubation flask, depending on the concentration of nitrate expected to be present in the environment. This actually led to enrichments ranging from 1 to 90% of natural concentrations. Immediately after isotope additions, samples were placed in the incubators for periods of 4–6 h. These periods represented a compromise to minimize both the effects of a decrease in isotope during incubation and the effects of initial surge uptake, which are factors that may create inaccuracies in N uptake estimates (Dugdale and Wilkerson, 1986). At the end of the incubation, each sample was divided into two parts. The first half was directly filtered on 21 mm pre-combusted Whatman GF/F (~0.7 μm), thus providing nitrogen uptake for the whole phytoplankton assemblage. The second half was sequentially filtered on 25 mm Poretics 5.0 μm and on pre-combusted GF/F filters, thus providing the uptake by the small size fraction (~0.7–5.0 μm). The filters were kept frozen until analysis. Analyses were performed on desiccated filters (dried for 6 h at 65°C), with a CN analyser coupled to a tracer mass spectrometer (Europa Scientific). This instrument measures the quantity of particulate organic nitrogen (PON) and the percent concentration of ^{15}N in the particulate organic matter at the end of incubation.

Size fractionation of natural populations, whether before or after incubation, inevitably leads to inaccuracies. On the one hand, post-incubation fractionation may overestimate the small fraction (biomass as well as nitrate uptake) because of the disintegration of some large cells. On the other hand, pre-screening may stress the cells before incubation (including cell breakage). Moreover, when nitrogen is

limiting, as is often the case in marine waters, there may be competition for this nutrient among the different size classes of phytoplankton. In such a case, removing one size class of phytoplankton before incubation could lead to totally unrealistic uptake rates. According to this, post-incubation filtration appears to be the method that minimizes the inaccuracies due to size fractionation and, for this reason, is the approach used in almost all published studies on natural phytoplankton.

Calculations

Specific nitrate uptake rates (h^{-1}) were calculated as:

$$Vn = \frac{(^{15}N_p - {}^{15}N_o)}{(^{15}N_d - {}^{15}N_o) \cdot T} \tag{1}$$

where $^{15}N_p$ is the concentration of ^{15}N (atom %) in the particulate phase after incubation, $^{15}N_o$ is the concentration of ^{15}N (atom %) in the particulate phase at time zero (i.e. natural concentration in the particulate phase), $^{15}N_d$ is the concentration of ^{15}N in the dissolved phase at time zero (i.e. following the ^{15}N enrichment) and T is the incubation time (h).

Transport rates (ρn, μmol N-NO$_3$ l^{-1} h^{-1}) were calculated as:

$$\rho n = PON_f \cdot Vn \tag{2}$$

where PON_f is the concentration of particulate organic nitrogen after incubation. Equation (1) is the same as equation (2) in Dugdale and Wilkerson (1986). Equation (2) is the same as equation (4) in Collos (1987). These give the uptake rates for the whole assemblage and for the small size fraction. Uptake rates for large phytoplankton were obtained by subtraction: whole assemblage – small fraction.

Results

Hydrographic conditions and concentrations of nitrate

In spite of different depths and locations, the time–depth sections of σ_t were similar at the three stations (Figures 2a, 3a and 4a). Waters were stratified from July through October and destratified from November through June. Depths of the euphotic zone ranged between 20 and 54 m, without any obvious seasonal pattern. Water temperature (Figure 5) was <6°C until June (stations B and C) or July (station A), at which time it strongly increased to reach a maximum (>16°C) in August and September, followed by a decrease to minimum values in February and March (~2-4°C).

At station A (Figure 2b), nitrate concentrations were high at the surface in March and April (3.6 μmol N l^{-1}) and at the bottom of the euphotic zone in May and June (up to 6.5 μmol N l^{-1}). In summer, concentrations were low (generally <0.5 μmol N l^{-1}) and relatively homogenous over the euphotic zone. Nitrate started to increase in September and October, to reach high values (up to 6 μmol N l^{-1}) in February. Seasonal trends were similar at stations B and C (Figures 3b and 4b).
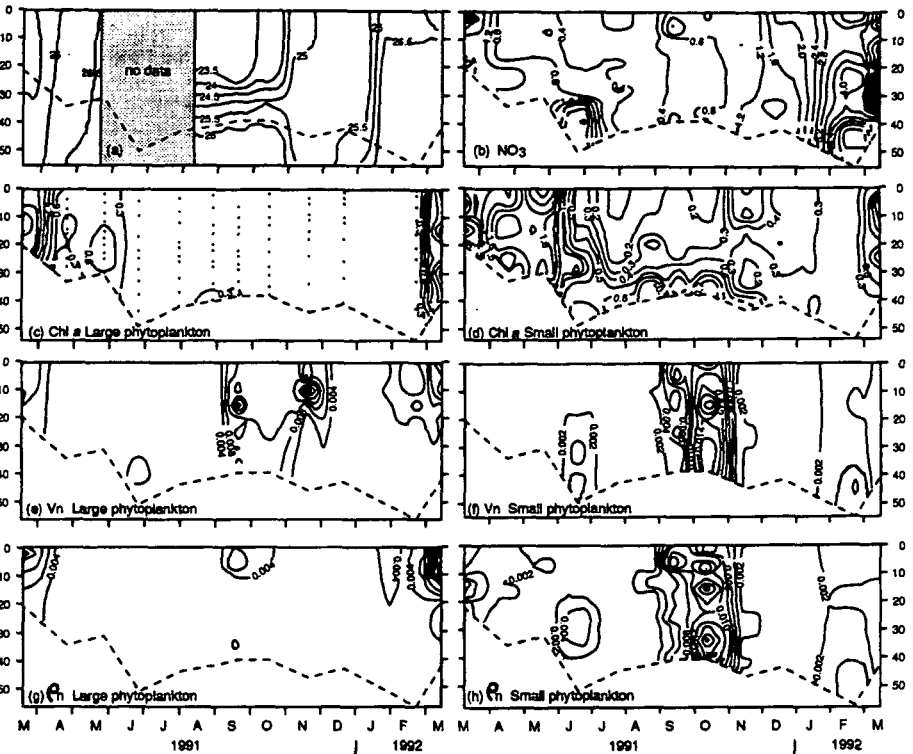
Fig. 2. Temporal variations at station A of (**a**) isopycnals; isopleths for (**b**) NO_3 (μmol N l^{-1}), chl a (μg l^{-1}) of (**c**) large and (**d**) small phytoplankton; nitrate specific uptake rate (Vn: h^{-1}) for (**e**) large and (**f**) small phytoplankton; and nitrate transport rate (ρn: μmol N l^{-1} h^{-1}) for (**g**) large and (**h**) small phytoplankton. Dashed lines: depth of the euphotic zone.

Chlorophyll a (chl a) concentrations

At station A (Figure 2c), a bloom of large phytoplankton (>5 μm) occurred in spring (March–April), with maximum annual values of chl a in the large size fraction up to 6.7 mg m^{-3}. During the remainder of the year, concentrations of chl a >5 μm ranged from 0.01 to 1.2 mg m^{-3}. A secondary maximum (up to 1.1 mg m^{-3}) was observed at the bottom of the euphotic zone in September. Stations B and C showed similar trends, with some slight differences, i.e. at station B (Figure 3c), there was an additional increase of biomass (up to 2 mg m^{-3}) at the bottom of the euphotic zone in June and July, and slightly higher values at the top in November (0.2 mg m^{-3}). At station C (Figure 4c), concentrations of chl a >5 μm at the bottom of the euphotic zone began to increase in September (0.57 mg m^{-3}), to reach a maximum value in October (1.2 mg m^{-3}). In November, values were higher than at any other time of the year, except during the spring bloom, over the entire euphotic zone.

Patterns of chl a <5 μm concentrations were not as clear as those of chl a >5 μm. At station A (Figure 2d), concentrations were high from March to June 1991, with a maximum in May (up to 2.0 mg m^{-3}), after which they decreased before increasing again in March 1992. There was also a small increase in November (up to 0.7 mg
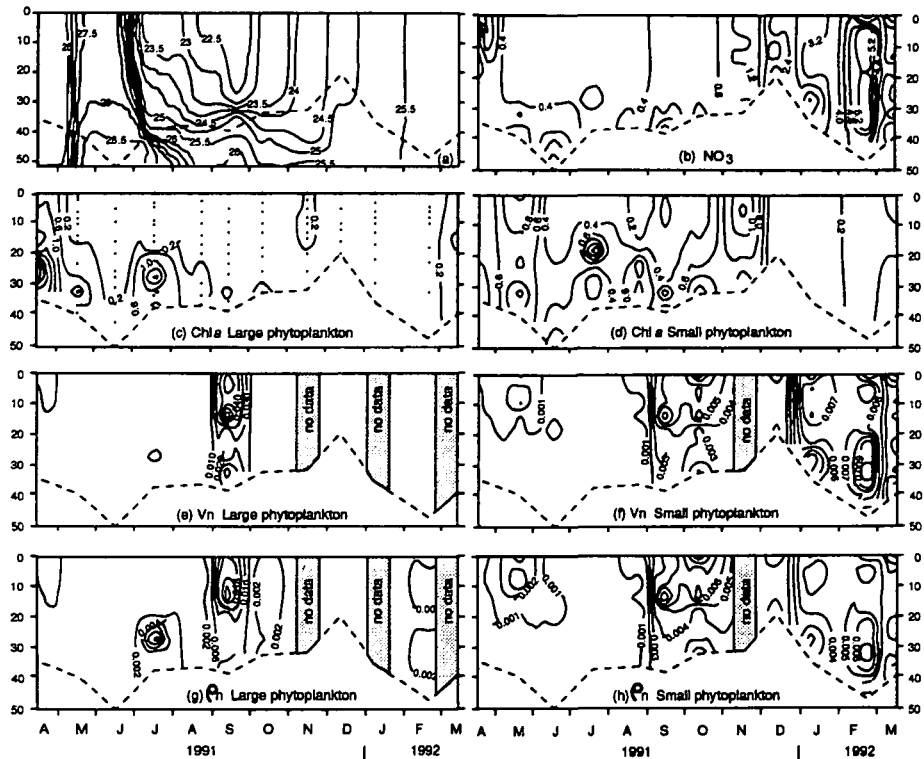
Fig. 3. Temporal variations at station B of (**a**) isopycnals; isopleths for (**b**) NO_3 (μmol N l^{-1}), chl a (μg l^{-1}) of (**c**) large and (**d**) small phytoplankton; nitrate specific uptake rate (Vn: h^{-1}) for (**e**) large and (**f**) small phytoplankton; and nitrate transport rate (ρn: μmol N l^{-1} h^{-1}) for (**g**) large and (**h**) small phytoplankton. Dashed lines: depth of the euphotic zone.

m^{-3}). Except during bloom periods, biomasses of small phytoplankton were higher and less variable over the year (0.05–2 mg m^{-3}) than those of large phytoplankton. During the spring bloom (March–April), chl a concentrations in the small fraction were lower than in the large fraction. In 1991, maximum chl a concentrations of small phytoplankton (2.0 mg m^{-3}, in May) occurred slightly later (~1 month) than those of large phytoplankton. At stations B and C (Figures 3d and 4d), the annual variations in chl a concentrations of small phytoplankton were roughly similar to those at station A. Because sampling at these stations started (in 1991) 1 month later than at station A and therefore at the end of the bloom (April), it is not possible to assert whether there was the same time lag at stations B and C as at station A between the blooms of large and small phytoplankton. In March 1992, the biomasses of large and small phytoplankton increased simultaneously.

Relative chl a in the small fraction was calculated for each sample (not shown). During the spring bloom (March–April), the ratio was <0.5 and quite constant over the euphotic zone at station A, but more variable with depth at station C. This was the period of the year with the lowest ratio (0.2 in March 1991 at station A), indicating that large phytoplankton accounted for most of the algal biomass. During the
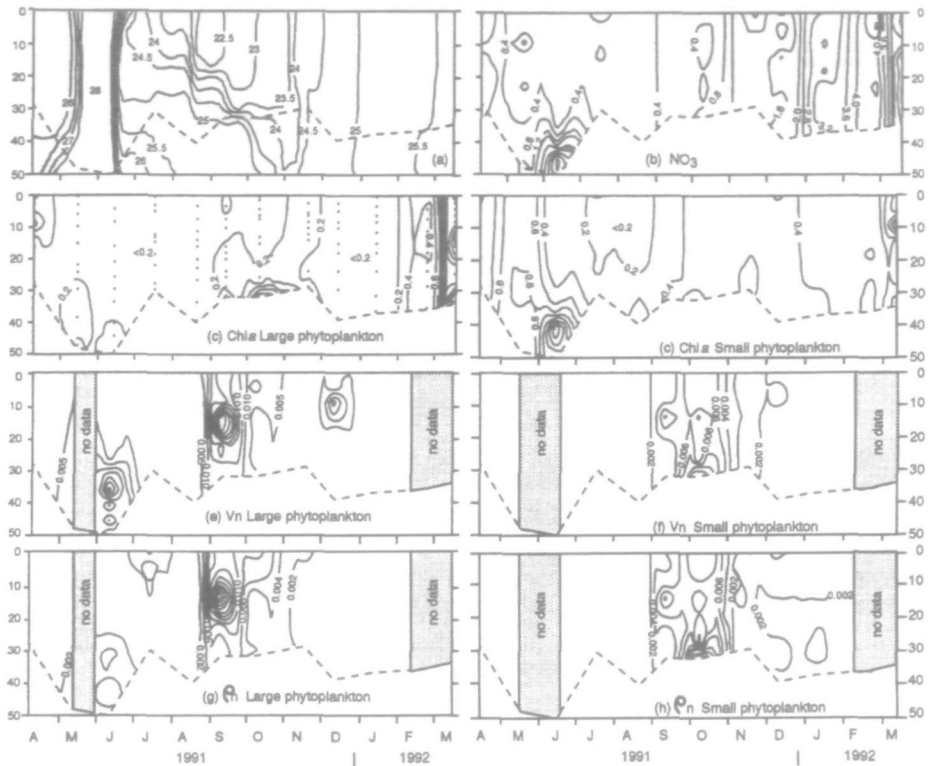
Fig. 4. Temporal variations at station C of (**a**) isopycnals; isopleths for (**b**) NO_3 (μmol N l^{-1}), chl a (μg l^{-1}) of (**c**) large and (**d**) small phytoplankton; nitrate specific uptake rate (Vn: h^{-1}) for (**e**) large and (**f**) small phytoplankton; and nitrate transport rate (ρn: μmol N l^{-1} h^{-1}) for (**g**) large and (**h**) small phytoplankton. Dashed lines: depth of the euphotic zone.

remainder of the year, phytoplankton <5 μm accounted for >60% of the total algal biomass.

Seasonal changes in size-fractionated phytoplankton biomass were summarized by integrating chl a concentrations over the euphotic zone (Table I). For phytoplankton >5 μm, a strong bloom occurred in both March 1991 and 1992 at station A, in April 1991 at station B, and in March 1992 at station C. During the remainder of the year, concentrations were low, with minimum values in summer. At stations B and C, there was a small increase in biomass in autumn (November at station B, and September and October at station C). This was not observed at station A. Differences between minimum and maximum values were large, i.e. from 1.7 to 112.1 at station A, 1.6 to 60.2 at station B, and 0.9 to 58.8 mg m^{-2} at station C.

For the <5 μm fraction, annual variations in depth-integrated chl a showed the same general pattern as for large phytoplankton, i.e. a spring bloom followed by minimum values during summer. However, there were two differences compared to the >5 μm fraction. The spring maximum was in May instead of March and the range from minimum to maximum values was smaller than for the large fraction, i.e. from 9.9 to 46.0 mg m^{-2} at station A, 5.8 to 29.7 mg m^{-2} at station B, and 5.9 to 34.7 mg m^{-2} at station C. Except in March (also April 1991 at station B and
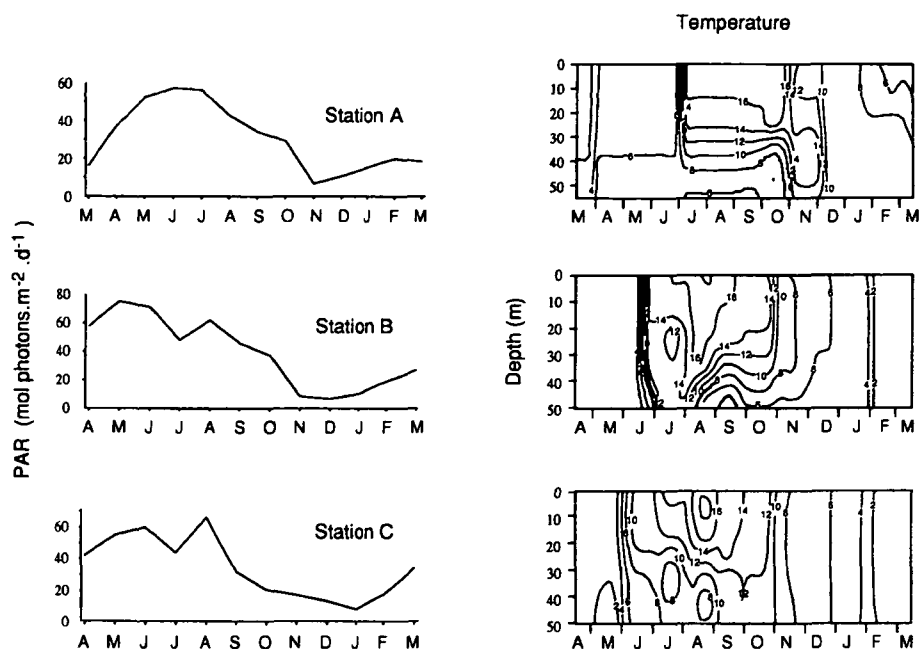
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Fig. 5. Temporal variations of photosynthetically active radiation (PAR), recorded at the meteorological station of Sable Island (one value for each sampling date, average of 3 days) and of the depths of isotherms, for the three stations.

February 1992 at station C), phytoplankton <5 μm accounted for >50% of total chl *a*, with values up to 90%.

Nitrate specific uptake and transport

Nitrate transport rates normalized to chl *a* were plotted as a function of NO_3 concentration (Figure 6) and water temperature (Figure 7). Visually, in all cases but one (station B, small fraction), there were no relationships between normalized nitrate uptake and nitrate concentration. Concerning water temperature, in spite of a lack of linear relationships, there was a general trend for the highest rates to occur at the highest temperatures, except for small phytoplankton at station B. Pairwise linear correlations were sometimes slightly different from visual interpretations (Table II). Normalized nitrate uptake rates were not correlated to nitrate concentration, except at station B for small phytoplankton (strong positive relationship) and at station C for large phytoplankton (weak negative relationship). Concerning water temperature, the only significant correlation for small phytoplankton was at station A (strong positive relationship), whereas correlations were all positive for large phytoplankton.

The temporal and vertical distributions of specific uptake rates were roughly similar at the three stations. *Vn* for phytoplankton >5 μm was maximum in autumn (Table II; Figures 2e, 3e and 4e). A secondary maximum was observed in March at station A, but not at stations B and C because of a gap in sampling. At station A, there was an increase in *Vn* at the bottom of the euphotic zone, in June. Patterns of

Table I. Vertically integrated chl *a* concentrations (mg m⁻²) for the large and small size fractions, relative contribution of small phytoplankton to total chl *a* and depth of the euphotic zone (*Ze*)

Station	Month	>5 μm	<5 μm	<5 μm/total (%)	*Ze* (m)
A	March 1991	112.1	22.7	16.8	20
	April 1991	7.7	46.0	85.7	33
	May 1991	17.3	47.6	73.4	30
	June 1991	5.1	24.6	82.9	49
	July 1991	2.7	9.9	78.5	37
	Aug. 1991	4.2	15.3	78.4	40
	Sept. 1991	3.8	10.9	74.3	38
	Oct. 1991	1.7	11.8	87.6	38
	Nov. 1991	3.9	14.6	78.8	44
	Dec. 1991	5.7	12.5	68.7	41
	Feb. 1992	4.9	12.5	71.8	54
	March 1992	74.3	31.5	29.8	40
B	April 1991	60.2	14.8	19.8	35
	May 1991	16.5	31.3	65.5	40
	June 1991	6.2	12.2	66.4	51
	July 1991	24.2	19.4	44.4	38
	Aug. 1991	4.2	17.3	80.5	37
	Sept. 1991	4.3	12.3	74.2	39
	Oct. 1991	3.1	18.0	85.3	33
	Nov. 1991	6.2	29.7	82.7	32
	Dec. 1991	3.0	5.8	66.0	20
	Jan. 1992	1.6	10.2	86.6	36
	Feb. 1992	5.3	6.2	54.1	48
	March 1992	10.7	8.8	45.1	40
C	April 1991	6.7	6.7	50.0	28
	May 1991	9.0	34.7	79.4	48
	June 1991	4.4	32.4	88.1	50
	July 1991	1.0	5.9	86.0	30
	Aug. 1991	0.8	8.6	91.0	40
	Sept. 1991	7.3	9.5	56.6	32
	Oct. 1991	7.6	16.6	68.8	32
	Nov. 1991	5.8	12.4	68.2	29
	Dec. 1991	3.5	17.5	83.2	39
	Jan. 1992	3.0	13.7	82.1	37
	Feb. 1992	12.8	6.9	35.1	36
	March 1992	58.8	17.4	22.8	34

variation for the <5 μm fraction (Figures 2f, 3f and 4f) were the same as for large phytoplankton. Maximum specific uptake rates also occurred in autumn, except at station B (maximum in January; Table II). At station A, there were secondary increases in March 1992 and at the bottom of the euphotic zone in June (missing data at stations B and C). For the two size fractions, the spring peak in *Vn* values coincided with high biomasses. This was not the case for high autumn (stations A and C) and winter (station B) *Vn*, which corresponded to low biomasses.

Annual and temporal distributions of transport rates (ρn) ran parallel to those of *Vn*. At station A (Figure 2g), the transport rate of cells >5 μm was maximum in March 1992, and at station B and C in September (Figures 3g and 4g; Table III).
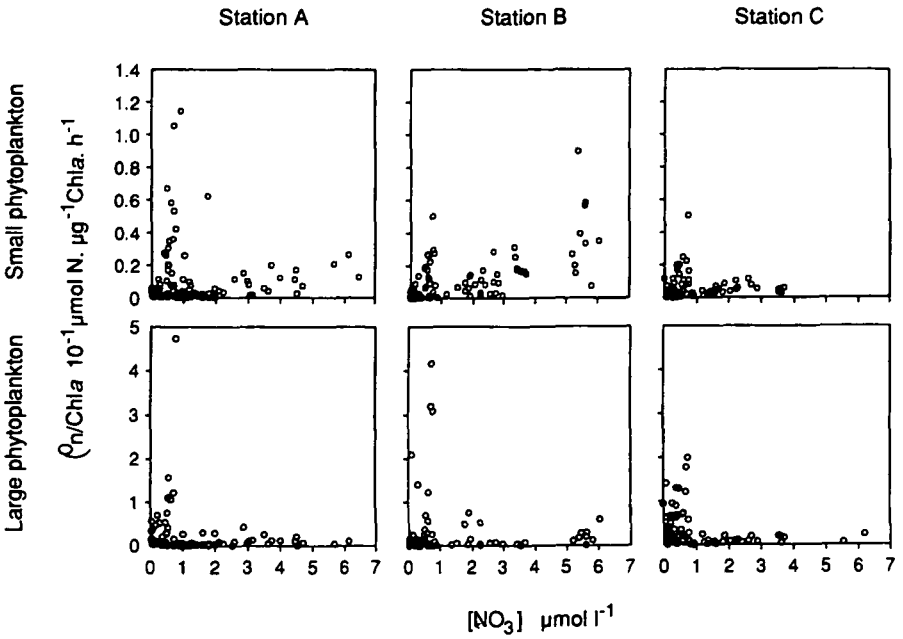
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Fig. 6. Normalized nitrate transport rates as a function of nitrate concentration, for small and large phytoplankton, at the three stations.
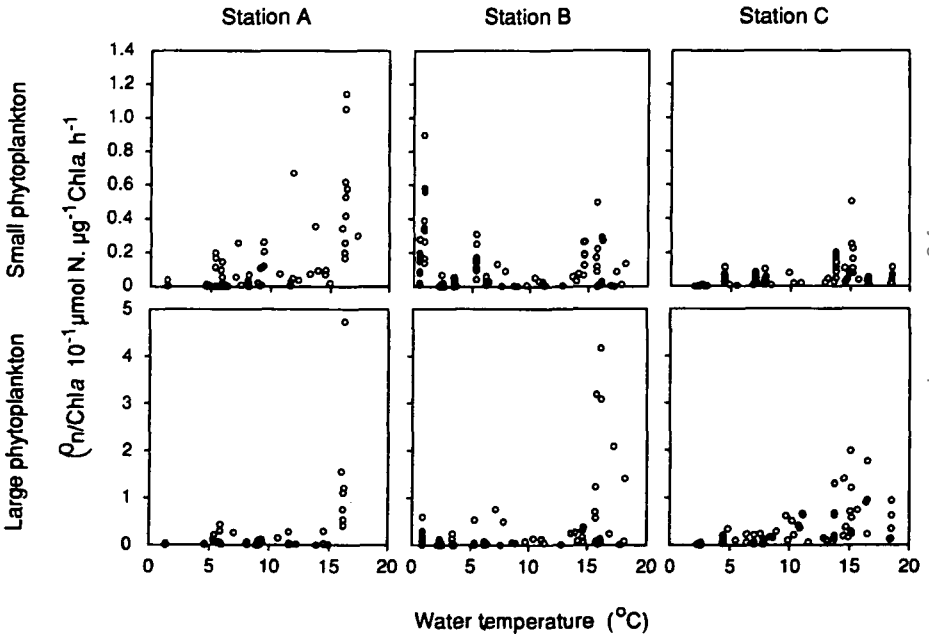
Fig. 7. Normalized nitrate transport rates as a function of water temperature, for small and large phytoplankton, at the three stations.

Table II. Pairwise linear correlations between pn/chl a and nitrate concentration, and between pn/chl a and water temperature (°C), for the three stations

	Station	Correlation (r)	P
Small phytoplankton			
pn/chl a versus NO$_3$	A	0.01	>0.05
	B	0.64	<0.05
	C	0.14	>0.05
pn/chl a versus temperature	A	0.59	<0.05
	B	−0.16	>0.05
	C	0.08	>0.05
Large phytoplankton			
pn/chl a versus NO$_3$	A	−0.04	>0.05
	B	−0.05	>0.05
	C	−0.29	<0.05
pn/chl a versus temperature	A	0.41	<0.05
	B	0.36	<0.05
	C	0.54	<0.05

For small phytoplankton, values were maximum in autumn at the three stations (Figures 2h, 3h and 4h; Table III). Transport rates normalized to chl a for the <5 μm fraction were maximum in October at stations A and C, and in February at station B. For large phytoplankton, the rates were maximum in September at the three stations (Table III).

Hourly transport rates were converted to daily values (i) by dividing them by the fraction of daily irradiance represented by the hourly irradiance at sampling time after which (ii), assuming a dark/light uptake ratio of 0.1 for NO$_3$ (Probyn, 1988), dark N uptake rates were calculated by multiplying the N hourly uptake rates by 0.1 and by the duration of the dark period (in h). Daily N uptake rates are the sum of (i) and (ii). These were then integrated over the euphotic zone and, assuming that estimated daily rates were the same over the sampling month, were turned into monthly values by multiplying the daily rates by the number of days in each month (Table IV). Missing data were interpolated.

Trends in monthly transport rates were the same as described above for Vn with, at station A, two maxima: the first in spring and the second in autumn (Figure 8). At stations B and C, transport rates peaked in autumn only. At station A, the maximum transport rate in spring accounted for up to 33% of the annual total (%pni; Table IV). At this time, the large fraction was responsible for most of the nitrate transport (%pni_L; Table IV). Transport rates during autumn accounted for up to 55% of the annual value (%pni in September–October 1991, at station C). In this case, the transport of nitrate was mainly due to small phytoplankton at stations A and C in October, and to large phytoplankton at stations B and C in September (%pni_S and %pni_L; Table IV). Between 58 and 68% of the total annual nitrate transport (large + small fractions) occurred during these 3 months, i.e. March, September and October. The relative contribution of small phytoplankton to

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Table III. Maximum nitrate specific uptake rates (Vn: h^{-1}), transport rates (ρn: mmol N m^{-3} h^{-1}) and ρn/chl a (mmol N h^{-1} mg^{-1} chl a), for the two size fractions

		Station	Maximum	Date
Fraction < 5 μm				
	Vn	A	0.026	Oct. 1991
		B	0.012	Jan. 1992
		C	0.046	Oct. 1991
	ρn	A	0.028	Oct. 1991
		B	0.012	Sept. 1992
		C	0.036	Oct. 1991
	ρn/chl a	A	0.114	Oct. 1991
		B	0.090	Feb. 1992
		C	0.684	Oct. 1991
Fraction > 5 μm				
	Vn	A	0.071	Nov. 1991
		B	0.084	Sept. 1991
		C	0.073	Sept. 1991
	ρn	A	0.079	March 1992
		B	0.029	Sept. 1991
		C	0.036	Sept. 1991
	ρn/chl a	A	0.887	Sept. 1991
		B	0.417	Sept. 1991
		C	0.200	Sept. 1991

transport rate (%ρn_S; Table IV) was >50% of the total nitrate transport during at least half of the year at stations B and C, and for a longer period at station A. Large phytoplankton were clearly dominant during spring at station A (interpolated values at stations B and C), but the situation was not as clear cut in autumn (Figure 8). At this time of the year, small phytoplankton were dominant at station A, whereas large phytoplankton were dominant at station B. At station C, large and small phytoplankton were successively dominant. For the whole year, the small size fraction accounted for 44 (stations B and C) to 62% (station A) of total nitrate transport.

Discussion

Temporal and vertical distributions of large and small phytoplankton

There was a major spring bloom, dominated by large phytoplankton, at the shelf break (station A) and on the shelf (stations B and C) (Table I). The bloom took place at times of high NO$_3$ concentration (~3.5 μmol N-NO$_3$ l^{-1}). This corresponds to the classical situation and probably resulted from the seasonally increasing stratification of the water column and irradiance (Riley, 1942; Sverdrup, 1953; Legendre, 1990). On the shelf, there was a secondary autumn bloom (lower than in spring), which was dominated by small phytoplankton (Table I). The autumn bloom was not apparent at the shelf break. However, at the three stations, specific NO$_3$ uptake and transport rates were generally high in spring and autumn, reflecting active phytoplankton growth (Table III; Figure 8). Consequently, it is likely

Table IV. New production: $\%\rho ni$ is the ratio (%) of new production for a given month to the annual value (ρn_T month/ρn_T annual); $\%\rho ni_L$ and $\%\rho ni_s$ are the same as ρni, but for the large and small phytoplankton, respectively; $\%\rho n_s$ is the ratio (%), for a given month, of <5 μm to total new production (ρn_s month/ρn_T month)

| Station	Month	$\%\rho ni$	$\%\rho ni_L$	$\%\rho ni_s$	$\%\rho n_s$
A	March 1991	12.9	11.5	1.4	10.6
	April 1991	1.9	0.3	1.6	85.3
	May 1991	3.7	1.8	1.9	51.9
	June 1991	8.5	2.5	6.0	70.4
	July 1991	3.1	2.2	0.9	29.0
	Aug. 1991	4.2	1.5	2.7	63.9
	Sept. 1991	13.4	4.9	8.5	63.3
	Oct. 1991	33.3	8.7	24.6	74.0
	Nov. 1991	2.7	0.7	2.0	74.2
	Dec. 1991	1.3	0.5	0.8	59.6
	Jan. 1992	5.4	1.4	4.1	74.5
	Feb. 1992	9.6	2.3	7.4	76.5
A	April 1991	1.5	0.2	1.3	85.3
	May 1991	2.9	1.4	1.5	51.9
	June 1991	6.6	2.0	4.7	70.4
	July 1991	2.4	1.7	0.7	29.0
	Aug. 1991	3.3	1.2	2.1	63.9
	Sept. 1991	10.4	3.8	6.6	63.3
	Oct. 1991	25.9	6.8	19.2	74.0
	Nov. 1991	2.1	0.5	1.6	74.2
	Dec. 1991	1.0	0.4	0.6	59.6
	Jan. 1992	4.2	1.1	3.2	74.5
	Feb. 1992	7.5	1.8	5.7	76.5
	March 1992	32.1	30.1	2.0	6.2
B	April 1991	4.5	3.6	0.9	20.6
	May 1991	3.8	1.1	2.7	71.5
	June 1991	2.8	1.3	1.5	53.3
	July 1991	6.1	5.6	0.5	7.8
	Aug. 1991	1.9	0.9	1.0	54.5
	Sept. 1991	32.4	24.0	8.5	26.1
	Oct. 1991	8.7	1.7	7.0	80.2
	Nov. 1991	5.1	1.1	4.0	77.8
	Dec. 1991	1.5	0.5	0.9	63.8
	Jan. 1992	8.2	2.3	5.9	71.9
	Feb. 1992	15.2	4.1	11.1	73.3
	March 1992	9.8	3.8	6.0	61.0
C	April 1991	0.6	0.4	0.2	35.7
	May 1991	5.2	4.5	0.7	13.5
	June 1991	9.3	8.6	0.7	7.6
	July 1991	4.7	3.5	1.2	25.2
	Aug. 1991	2.4	1.1	1.3	55.6
	Sept. 1991	31.5	22.3	9.2	29.2
	Oct. 1991	23.4	7.6	15.8	67.3
	Nov. 1991	3.8	1.4	2.4	62.8
	Dec. 1991	6.1	1.8	4.4	71.1
	Jan. 1992	6.1	2.1	4.0	65.1
	Feb. 1992	3.4	1.3	2.1	62.3
	March 1992	3.4	1.3	2.1	62.3

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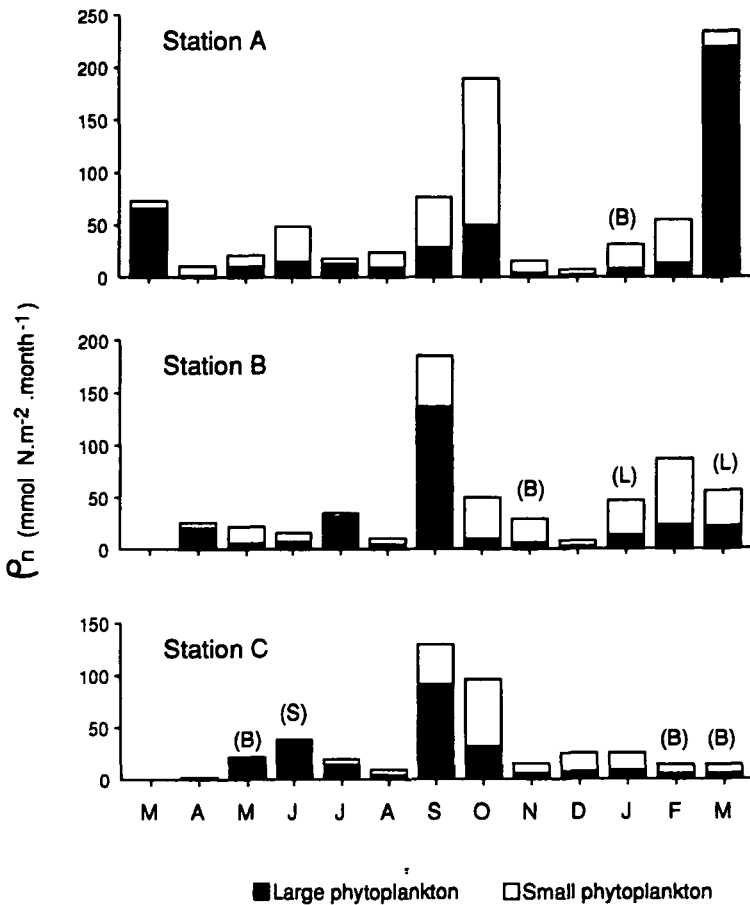
Fig. 8. Monthly values of vertically integrated nitrate transport rates (mmol N m^2 month^{-1}), for phytoplankton >5 and <5 μm, at stations A, B and C. (B) Values for both large and small phytoplankton initially missing and interpolated (i.e. averaged) from values of the previous and following months. (L) and (S) Only the value for large or small phytoplankton was initially missing and interpolated.

that high phytoplankton growth in autumn occurred not only on the shelf, but also at the shelf break, where the lack of high biomass in autumn probably reflected strong grazing. This is consistent with the study of Fournier *et al.* (1977), who found increased microzooplankton concentration in autumn in this area.

Vertical and temporal distributions were not as different between large and small phytoplankton as generally assumed (e.g. Goldman, 1988; Cushing, 1989). The vertical distributions of chl *a* in the euphotic zone (Figures 2, 3 and 4) were generally similar for the two size fractions, with maximum values at approximately the same depths. The situation was less clear for temporal variations since, in spring 1991 at the shelf break, maximum concentrations of chl *a* for the small and large phytoplankton were slightly separated in time. On the shelf, because of the late start of the sampling programme, it is not possible to assert whether there was a similar lag. It is thus likely that, in 1991, large and small phytoplankton responded

differently to spring changes in environmental factors (e.g. stability of the water column, nutrient concentrations, irradiance, water temperature). With our data set, it is difficult to determine to which factor(s) the large and small cells did respond differently in 1991, given the finding that the two size fractions increased simultaneously in March 1992 (Table I) with no obvious difference in environmental factors compared to March 1991.

To sum up the situation on the Scotian Shelf, maximum biomasses for large and small phytoplankton both occurred during spring, but these were separated by 1–2 months in 1991 (perhaps not in 1992). The abundances of the two size fractions often tended to covary with respect to depth. Hence, the ecosystem was characterized by a background of small algae, onto which the spring bloom of large phytoplankton was superimposed.

Specific uptake and transport rates of nitrate: seasonal variations and size partitioning

It is likely that, most of the time, nitrate was not limiting phytoplankton production on the Scotian Shelf. First, 66% of nitrate values were $>0.50 \mu mol N l^{-1}$, which is the half-saturation constant given by Dortch and Postel (1990). Moreover, in all cases but two, there was no relationship between normalized nitrate uptake rate and nitrate concentration (Figure 6, Table II). When there was a linear relationship, it was either strongly positive (station B, small phytoplankton) or weakly negative (station C, large phytoplankton), without any obvious explanation. According to Le Bouteiller (1986), a lack of relationship between Vn and nitrate concentration should indicate lack of phytoplankton limitation by NO_3. In the present study, the highest nitrate uptake did not correspond to the highest nitrate concentrations (Figure 6), but instead to the relatively low concentrations observed in September and October (Figures 2–4). Annually, the highest Vn values and the beginning of the annual increase in nitrate concentrations occurred in the autumn months (Figures 2, 3 and 4). Even though time scales are very different, these results are consistent with those of Glibert and Garside (1992), who worked on diel variability in N-nutrient uptake in Chesapeake Bay. They reported weak correlations between uptake rates and availability of NO_3, and suggested that 'availability or flux of a particular nitrogen substrate *per se* was insufficient to produce the observed diel patterns in uptake'. Results of the present study (Figure 6; Table II) lead to the same conclusion, at the annual scale. This indicates that environmental factors other than nitrate concentration (e.g. irradiance and/or water temperature) are also important for the uptake of nitrate.

In August, water temperature was maximum, but nitrate concentration was low, which impeded nitrate uptake. In September, water temperature was still high (15–16°C) and, at the same time, NO_3 concentration increased, which favoured phytoplankton production. During the spring bloom, low temperature (1–1.5°C) seemed to play an opposite role, i.e. in spite of high nitrate concentration and high irradiance, nitrate specific uptake and transport rates were lower than in autumn. Given that cold temperature can inhibit NO_3 uptake (Glibert and Garside, 1992) and that irradiance was quite similar in early spring and autumn (Figure 5), temperature was probably the environmental factor responsible for the relatively low

nitrate uptake in springtime (see Table II, and Figures 5 and 7). Factors other than water temperature and irradiance can also influence nitrate uptake. Recent studies reported that either P (Schelske, 1994), Si (Dugdale and Wilkerson, 1994) or Fe (Timmermans *et al.*, 1994), when deficient, could limit nitrate uptake. However, our data did not corroborate these ideas. On the Scotian Shelf, PO_4 and Si were minimum in August and September (~ 0.2 and 1.0 mmol m^{-3}, respectively, not shown) and began to increase in October. Since nitrate uptake was very high in September, it seems unlikely that these nutrients limited nitrate uptake. Concerning Fe, Martin *et al.* (1993) found no evidence of deficiency in the North Atlantic.

As in many other marine areas, there was a spring bloom of large phytoplankton on the Scotian Shelf, with correspondingly high nitrate transport (Figures 2c and 8). Our results show that, at station A, ~ 13–32% of the annual new production ($\%\rho ni$; Table IV) took place during the spring bloom of large phytoplankton and that phytoplankton >5 μm accounted for most of it. Around 60% of the nitrate uptake in spring at stations B and C, and 90% at station A, were due to large phytoplankton. This seems to be consistent with the classical tenet associating large phytoplankton with the uptake of new nitrogen, but needs to be qualified since nitrate transport of the <5 μm fraction also increased during the bloom of large phytoplankton. At station A, the spring bloom of the <5 μm fraction (June 1991, for nitrate transport rates) was responsible for $\sim 5\%$ of the total annual new production ($\%\rho ni_s$, Table IV). In the same way, and even if no bloom was apparent from chl *a* concentrations, increased uptake rates led to high nitrate transport by both large and small cells in autumn (up to 200 mmol N m^{-2} month^{-1} in September on the Shelf, and in October at the shelf break). Around 10% of the annual new production occurred in September and $\sim 30\%$ in October ($\%\rho ni$; Table IV). At that time, new production was often mainly due to small phytoplankton (63–74% at station A, 26–80% at station B, and 29–67% at station C for September and October, respectively).

The partitioning of nitrate uptake and transport between large and small phytoplankton (Table IV) showed dominance by the >5 μm fraction in spring. The situation was not as clear in autumn, when $\%\rho n_s$ varied according to month (September or October) and station (Figure 8). During the remainder of the year, the relative nitrate transport rate of small phytoplankton tended to be >0.5 (ρn_s $>50\%$; Table IV), i.e. most of the new production was due to the small size fraction. For the whole year, the small phytoplankton were responsible for about half of the total new production (44–62%).

It follows from the above results that the difference between large and small phytoplankton in taking up new nitrogen is less clear cut than currently thought. This leads us to qualify the classical association of large phytoplankton with new production. Our results suggest that, during the spring bloom, most of the new production was due to large phytoplankton (Figure 8). The situation was often reversed in autumn, when small phytoplankton generally had high nitrate uptake rates (Figure 8). During the remainder of the year, at least half and often up to 80% of new production was due to the <5 μm fraction (Table IV). Even if our results are somewhat unusual, other studies have also reported a significant contribution of small phytoplankton to new production. For example, in the Mediterranean Sea,

Selmer *et al.* (1993) found that nitrate uptake, even though it was very low compared to that of ammonium, mostly took place in the smallest size fractions (<1 or 1–10 μm). Similarly, Probyn and Painting (1985) observed, in Antarctic surface waters, that the uptake of nitrate by phytoplankton <1 μm was sometimes equal to that of the 15–200 μm fraction.

Conclusion: ecological significance

New production on the Scotian Shelf was mainly due to small phytoplankton, except during bloom periods. The spring bloom of large and small cells was superimposed on a background concentration of small phytoplankton. Outside the bloom period, phytoplankton biomass consisted of a rather steady concentration of small phytoplankton and large phytoplankton in very low abundance (Figures 2, 3 and 4c and d). On the vertical axis, most of the time, there were no obvious differences in the distributions of the large and small size fractions. Thus, our first hypothesis (i.e. large and small phytoplankton are segregated in time and space) is rejected.

Our results show that, on the Scotian Shelf, contrary to the classical tenet, large and small phytoplankton tended to have the same behaviour concerning nitrate uptake. In addition, because of the constant presence of small phytoplankton and despite Vn lower than that of the larger size fraction, the <5 μm algae accounted for a significant fraction (up to 60% on a yearly basis) of the new production. Thus, our second hypothesis (i.e. large phytoplankton are responsible for the bulk of new production) is also rejected.

The results of the present study suggest that the classical association of large phytoplankton with new production may not apply on the Scotian Shelf. The pattern of phytoplankton succession generally expected in temperate waters is, from spring to summer, a bloom of large cells followed by production of small cells. This succession is assumed to be driven by shifts in hydrodynamics (destratification and stratification) and in N-nutrient species (e.g. Margalef, 1978; Cushing, 1989). In the present study, the two size fractions tended to show the same spatial and temporal distributions, i.e. in most cases there was no visible phytoplankton succession (with respect to size). Moreover, large and small phytoplankton tended to have the same behaviour with respect to nitrate. Thus, rejection of our two hypotheses led to the conclusion that the classical pattern of seasonal succession in phytoplankton size distributions and nutrient control does not apply on the Scotian Shelf. Since the area does not differ markedly from other temperate shelves, our results open up the possibility that phytoplankton succession and nutrient control on these shelves do not follow the usually recognized pattern.

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